

FOSSIL AND RECENT COMATULID CRINOIDS WITH COELOMIC EXTENSIONS PENETRATING THE CENTRODORSAL

By AILSA M. CLARK

IN 1877 Ludwig published an anatomical study of the dorsal or chambered organ and associated structures of *Antedon rosacea* (i.e. *A. mediterranea* (Lamarck)) made on sections of decalcified material. He showed that there are five blind radial coelomic sacs extending from the coelom a short distance downwards (aborally) outside the chambered organ (see fig. 3j). On the oral (upper or ventral) face of intact centrodorsals of *Antedon* there are five radial depressions to house the ends of these sacs, which depressions are lacking in the majority of recent comatulids.

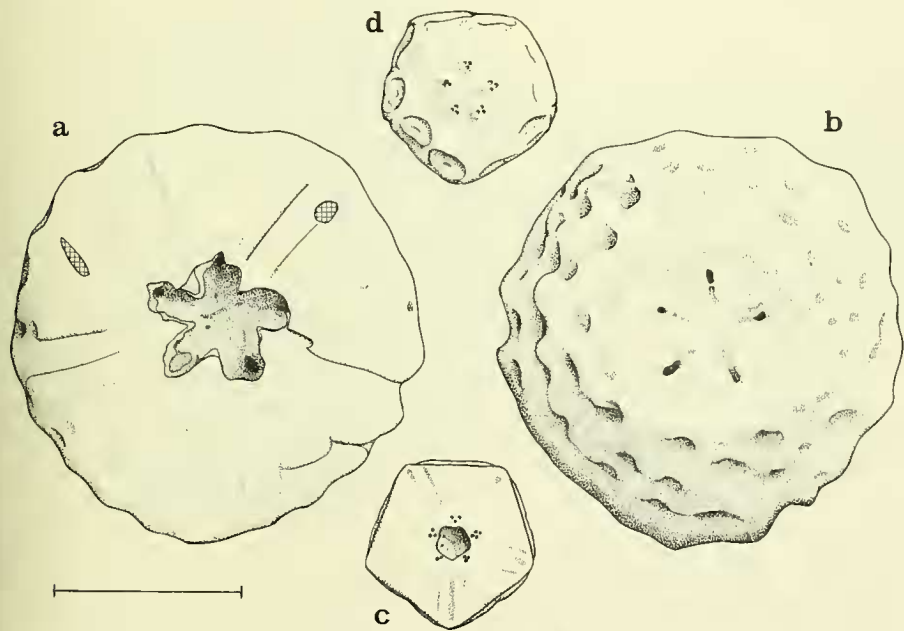


FIG. 1. a, b. †*Glenotremites paradoxus* Goldfuss. B.M. Palaeontological Department reg. no. E.297, Upper Chalk, Gravesend, Kent, centrodorsal after ultrasonic cleaning in ventral (a) and dorsal (b) views. c, d. The same of *Pterometra pulcherrima* (A. H. Clark). B.M. Zoological Department reg. no. 1972. 8.21.100, 'Anton Bruun' st. 18A, 07°34'N: 98°00'E (between Malaya and the Nicobar Islands), 77 metres. The scale measures 5 mm.

However, subsequent studies on some fossil comatulids and on recent members of the families Notocrinidae and Asterometridae, especially by Gislén (1924), have shown the presence in them of blind-ending radial pits in the centrodorsals housing similar but more extensive prolongations of the coelom. These pits open on the ventral face of the centrodorsal outside the cavity for the chambered organ unless that cavity is markedly lobate, when the perforations emerge at the extremities of the lobes, their much larger size differentiating them from the small apertures of the axial cords connecting the cirri to the chambered organ. The latter condition is found in the Cretaceous *Glenotremites paradoxus* Goldfuss (fig. 1a), which also has aboral radial openings situated in the lobes of a stellate hollow on the dorsal pole. Ultrasonic cleaning of a large centrodorsal of *G. paradoxus*, mentioned by Rasmussen (1961 : 292, no. 36) and by Gislén (1925 : 9, as *G. batheri*) has shown that these two sets of holes are the opposite ends of the same cavities. However, in none of the recent species so far sectioned, including *Notocrinus virilis* Mortensen, 1917, *Pterometra trichopoda* (A. H. Clark, 1908) and *Asterometra anthus* (A. H. Clark, 1907) have the cavities yet been shown to perforate the centrodorsal completely. It is possible that such a condition does exist in smaller specimens of *Notocrinus virilis*. Mortensen (1918) observed that a 'half grown' individual of this species showed a central pore on the dorsal pole ringed by five radially-placed pores, which he assumed did not fully penetrate the centrodorsal. Gislén (1924 : 129, fig. 196) illustrates the centrodorsal of Mortensen's specimen in dorsal view showing five additional inter-radial indentations on the small cirrus-free dorsal pole; his caption says 'the five black dots are radially arranged, nearly perforate the Cd, and are the continuations of the chambered organ, the five interradian rings are small pits only'. This assumption that the radial aboral openings are connected to the chambered organ is surprising in view of the fact that he also shows (fig. 199) a vertical section through a centrodorsal with a conical radial pit opening on the upper side but (apparently) ending further aborally than the chambered organ, while the angle of alignment of the pit points directly at the dorsal pole.

To check this point, serial horizontal sections were made through the decalcified calyx of a specimen of *Notocrinus virilis* with the centrodorsal c. 3.5 mm in diameter and therefore probably comparable in size with Mortensen's (the largest individuals have centrodorsal c. 10 mm across). The aboralmost of the sections show a complete absence of cavities except for a few of the small double axial cords leading to the more apical cirri (fig. 2a). As the central mass of nervous tissue forming the aboral 'floor' of the chambered organ appears in successive sections, so also do apertures in two radii representing the extremities of the longest radial pits but these are well spaced from the nervous capsule. In the centre of the capsule an opaque spot of tissue resolves itself into five small cavities (see fig. 2b), which are radial in position and represent the uppermost end of the atrophied connection between the chambers of the chambered organ and the larval stalk. As these open out into the chambers upwardly, the three other radial pits appear in the matrix of the centrodorsal. Towards the upper end of the chambered organ, the central core of it becomes more opaque and enlarged; this is the base of the axial organ which emerges on the ventral side of the chambered organ into the much divided coelom. The chambers contract

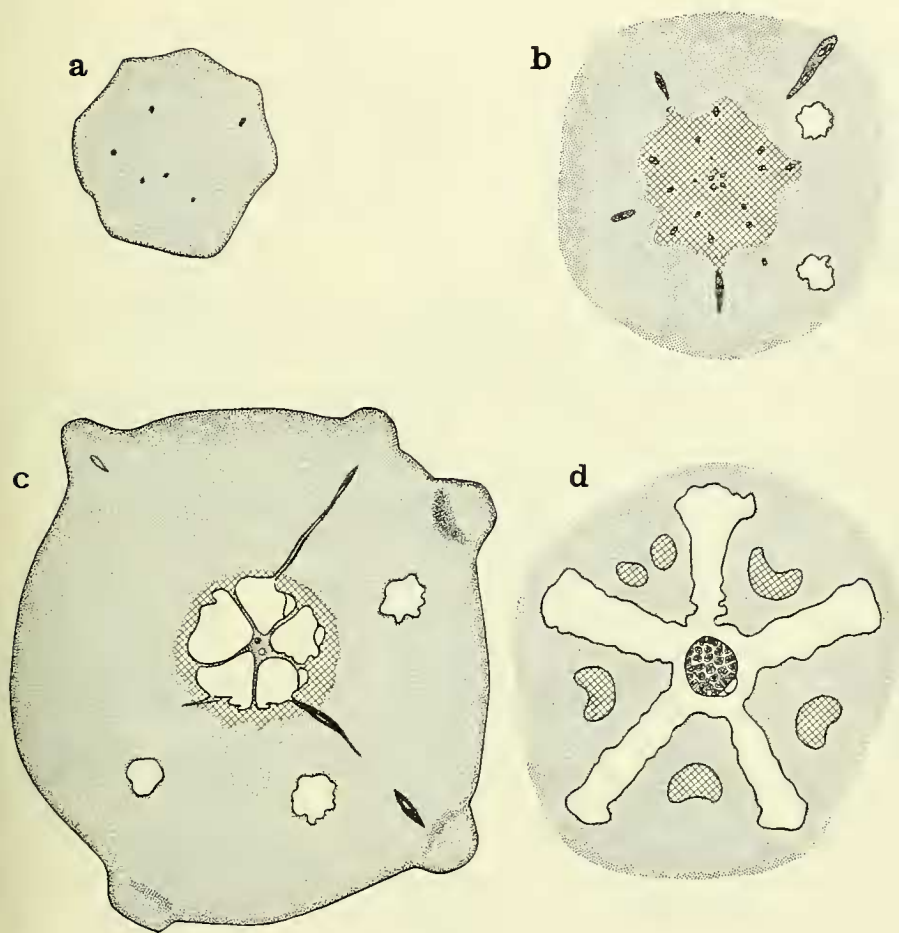


FIG. 2. *Notocrinus virilis* Mortensen. 1948.1.7.121, B.A.N.Z.A.R. Expedition st. 107, off MacRobertson Land, Antarctica, 219 metres, horizontal sections of decalcified calyx, original diameter of centrodorsal 3.5 mm. a. Section close to dorsal (aboral) extremity with only some obsolete axial cords to the more apical cirrus sockets interrupting the collagenous matrix (stippled); b. Nervous tissue (cross-hatched) forming the floor of the chambered organ showing the five small aboral extremities of the chambers centrally, with coelomic pits in two radii and oblique sections of axial cords; c. Lower part of chambered organ showing origin of two axial cords, a third radial pit having appeared; d. Axial organ in the centre, having emerged from the top of the chambered organ, with coelomic spaces around it linking horizontally to the upper ends of the radial pits in the centrodorsal. [In b and d the peripheral parts are omitted.]

sharply and the nervous tissue diverges obliquely ventro-laterally from them, dividing into five interrarial tracts which themselves soon split into two parts at the same time as the vertical radial pits give way abruptly to horizontal canals leading into the coelomic spaces around the axial organ (fig. 2d). The paired interrarial nerve tracts rapidly diverge and reunite radially, then are linked together horizontally by commissures forming the nerve ring, this in turn giving way to the five radial nerves leading to the arms. The whole arrangement of this aboral nervous system is very similar to that of *Antedon*, as illustrated by Hamann (1889, fig. on p. 65); the five circumscribed areas interrupting the direct link between the capsule of the chambered organ and the radial nerves leading to the arms serving to accommodate the radial coelomic sacs in *Antedon* and the comparable canals to the radial pits of the centrodorsal in *Notocrinus*.

A smaller centrodorsal (diameter 2.5 mm) of *N. virilis* decalcified and sectioned shows essentially the same limited extent of the radial pits. Also the untreated centrodorsal of another small specimen shows a somewhat pitted dorsal pole to the centrodorsal but without any particular regularity. I think that the apertures described by Gislén and supposed to connect with the larval stalk may have been due to similar erosion at the dorsal pole. Their existence needs to be checked by further sectioning of material at early ontogenetic stages.

This anatomical study of *Notocrinus* was in fact prompted by a large sample of *Pterometra pulcherrima* (A. H. Clark, 1909) taken off the coast of Burma at 'Anton Bruun' station 18A, which allowed several specimens to be sacrificed for anatomical study. This showed that, not only are the centrodorsals perforated on the ventral face in each radius, but also dorsally on five, radially-aligned, convexities on the dorsal pole, there being complete radial canals penetrating the centrodorsal (fig. 1c, d; also A.M.C., 1972, fig. 14). In this species, compared with *Notocrinus virilis*, the canals are not only more extensive but also multiple, with a cluster of up to four openings in each radius, though horizontal sections of decalcified specimens show that the divisions are irregular and incomplete, anastomosing at some levels into a single lobed canal only to separate again into separate parts, adding considerably to the surface area of the walls of the canals.

Although perforating the skeleton of the centrodorsal, these canals do not appear to open on the dorsal pole, the body wall being continuous across the mouth of each one. However, in a series of horizontal sections the cavities appear almost immediately within the five convexities of the dorsal pole and continue vertically to the level of the top of the chambered organ but outside it, though closer to it than the radial pits of *Notocrinus virilis*, causing the axial cords to the cirri to deviate more sharply around the radial canals.

The function of these coelomic extensions in the families Asterometridae and Notocrinidae (the Notocrinida of Gislén) remains to be determined. Professor Nichols (personal communication) has suggested that they are the probable sites of coelomocyte production. My thanks are due to him for this comment, also to Dr Jefferies of our Palaeontology Department, who suggested and carried out the ultrasonic treatment of the *Glenotremites*, and to Mr Cooper of the histological section of the Zoology Department, who made the sections.

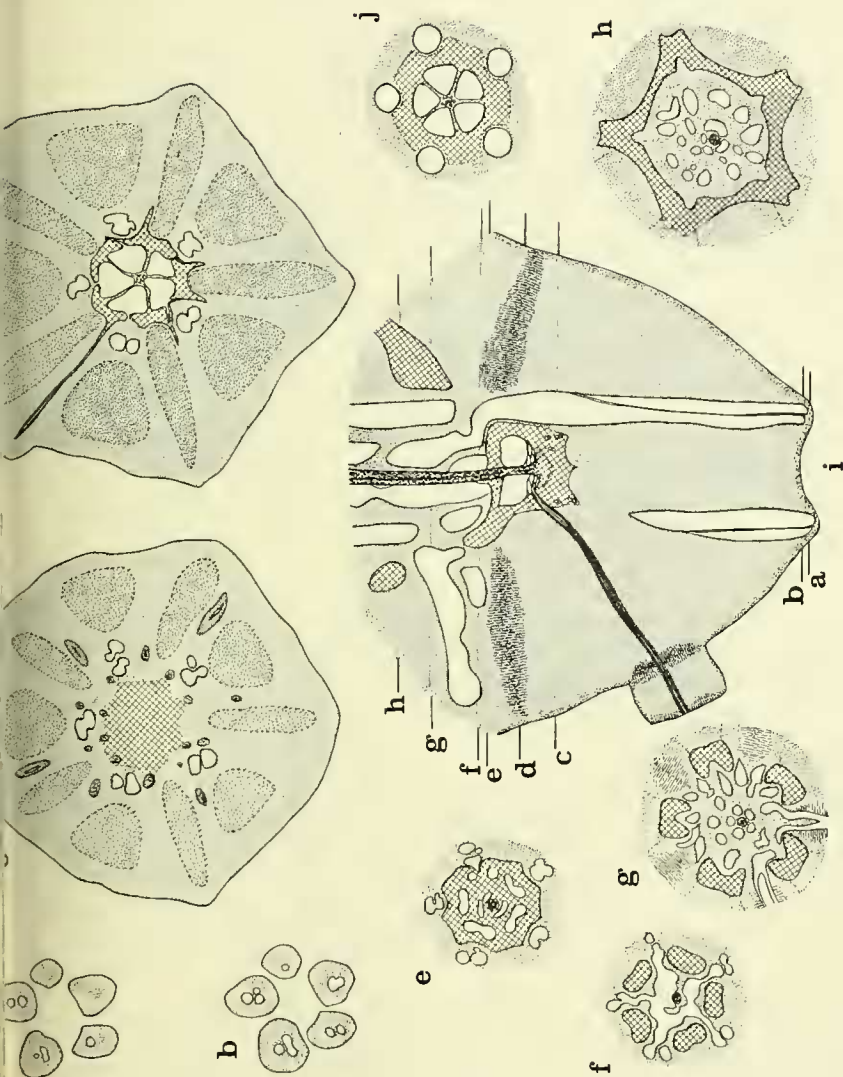


FIG. 3. a-i. *Pterometra pulcherrima* (A. H. Clark). [Details as in fig. 1, c, d]. Sections of decalcified calyces, original diameter of centrodorsal c. 4.5 mm., the levels of the horizontal sections (a-b) indicated on the vertical section (f), showing radial coelomic canals penetrating the centrodorsal to the convexities on the dorsal pole. In e, the base of the axial organ has appeared centrally with small coelomic pockets around it indenting the roof of the chambered organ; outside these the uppermost ends of the chambers are also visible while in one radius a coelomic canal is beginning its inward course to join up with the others around the

axial organ, as shown in f. In g and h, the coelom is further subdivided and the intraradial nerve trunks arising obliquely from the chambered organ have split and reunited radially and then become linked horizontally by commissures before giving off the five primary radial nerves. Compare the vertical section i with fig. 54 (p. 42) of Cuénot (1948) showing a similar section of *Antedon*. j. *Antedon mediterranea* (Lamarck), a decalcified horizontal section through the chambered organ [after Ludwig, 1877, pl. xiv, fig. 20.]

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AILSA M. CLARK
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD